GEOTROPISM IN ANIMALS[1]

By SAKYO KANDA
(From the Physiological Laboratory, University of Minnesota, Minneapolis)

I. The word "geotropism" was first invented by Frank, a German plant physiologist, in 1868 (19). The word "tropism" with prefix, helio, light, however, was first used by De Candolle, a French plant physiologist, in 1835 (39, p. 154). Tropism, as you all know, is a Greek word meaning "to turn." Geotropism is, therefore, "to turn" toward or away from the center of the earth or the force of gravity. Some writers use "geotaxis" instead of "geotropism." Taxis, a Greek word again, means "to arrange." According to them, "geotropism" is for plants which are not motile, and "geotaxis" for animals which are motile. But I prefer "geotropism" rather than "geotaxis" for the reason that the reactions of plants and animals, motile or not motile, to the force of gravity are fundamentally the same thing (cf. 40).

Many animals react to the force of gravity; most of them turn their anterior ends away from the center of the earth, and a few of them toward it. The former are called negatively, and the latter positively geotropic. The phenomena are negative and positive geotropisms.

Paramecium, for example, which is one of the unicellular organisms, orients itself with its anterior end upward, and swims in that direction; thus against gravity. Among the coelenterates, geotropism is shown by certain hydroids; by Antennularia antennina—a plant-like animal—for example, whose "stems" have a tendency to curve upward, and their "roots" a tendency to grow vertically downward, though the geotropic curvature of the "roots" is not so precise as in the "stems." The "roots," in this case, are positively, and the "stems" negatively geotropic. If you cut off a piece of the "stem," and reverse it, that is, place the "stem" end down

[1] This popular paper was read by the writer at the sixth annual meeting of the Minnesota Psychological Conference, which was held at the University of Minnesota, March 27, 1914. The text has not been changed since except to add foot-notes.

and " root " end up, it will regenerate " roots " at the lower end of the piece, which having been the " stem " end, would normally have grown upward, and will regenerate a " stem " at its upper end (31, pp. 494-495). Now, the question arises: what makes the animal orient itself toward or away from the force of gravity?

II. For students of physiology all animals, human animals inclusive, are " chemical machines " in which extremely complex processes are going on. Naturally, therefore, physiologists have attacked the problem of orientation of animals by gravity from a purely physical and chemical viewpoint. Ever since Schwarz first took up the problem in 1884, in unicellular organisms, bacteria, Euglena, Chlamydomonas, Desmid, Paramecium, and Spirostomum, have been subjected to quite extensive experiments for this purpose. Unfortunately, however, different investigators have offered varying explanations for the phenomena, though this problem we feel, is nearly settled now.[2] Limited time and space, however, prevent our dwelling on it here. We shall therefore simply refer to the names of various theories, namely, mechanical theory, pressure theory, resistance theory, and statocyst theory.

The first three theories as applied to unicellular organisms, having been experimentally shown to be fallacious, E. P. Lyon, in 1905, suggested the last theory. He applied to the unicellular forms, the ideas previously advanced by Goltz, Mach, Breuer, Bethe, Loeb, Verworn, and many others to explain orientation in the higher forms. Lyon's view was based on some experimental results, tending to show that the paramecium contains protoplasmic materials of different specific gravities.[3] " For internal stimulation," according to him, " the relation of the parts of the cell to each other must be changed in some way by gravity. Stresses or pulls which occur when the organism is in one position with respect to the vertical, must be changed in another position " (33, p. 429).

To illustrate the point, let us take some experimental examples. Eggs of sea-urchin, annelids, frogs, etc., when strongly centrifuged, separate into three layers, i. e., light, middle, and heavy.[4] There is no doubt, therefore, that dif-

[2] *Cf.* 24 and 34. The writer is also preparing a paper, " Further studies on the geotropism of Paramæcium caudatum and a direct proof that the animal contains protoplasmic materials of different specific gravity," in which he will attempt to settle this problem.

[3] The writer's recent experiments, not yet published, on Paramæcium caudatum, furnish direct evidence to prove that it is the case.

[4] E. P. Lyon was first to show these results (34).

ferences in specific gravity exist in the protoplasm of the animal cells. As has already been pointed out, the view of the statocyst theory of geotropism in paramecium accords with that of higher animals. Some crustacea, Palaemonetes, for example, have "irregular grains of sand mingled with other fine mineral particles and organic detritus" "in the basal segment of the antennule," which are the statoliths[5] for the organisms. The statoliths in question play an important rôle in the geotropic orientation of the organism. This has been proved by Prentiss' experiments as follows:

The statoliths are removed from the sacs of Palaemonetes by lifting the lid which covers the aperture, and forcing a fine jet of water into the cavity. Most of the sand having been thus washed out, the animals are placed in an aquarium upon the floor of which iron filings have been scattered and are allowed to remain until the iron particles have been taken into the sac in place of grains of sand. The shrimps (Palaemonetes) are blinded by painting the eyestalks with a mixture of lampblack and shellac. A *strong* electromagnet is then used. The pointed end of the magnet is held about 3 cm. from the statocysts, at one side of and a little ventral to them. Animals with normal statoliths, if blinded, do not respond at all, and are apparently unaffected by the proximity of the magnet; they keep their normal position, dorsal side up, with the sagittal plane of the body coincident with the direction of gravity. If not blinded, they simply move slowly away from the magnet when it approaches too near. When, however, the magnet is brought into close proximity to statocysts containing iron filings, the dorsal side of the animal is turned, not toward the magnet, as might be expected if the changed position were due directly to the action of the magnet on the iron filings, but away from it. If the magnet is changed to a position on the other side of the shrimp, the turning is in the opposite direction, still away from the source of attraction (39, p. 239). "There is only one explanation for this turning of the body away from the attracting force, and that is a very simple one. Under normal conditions the body of the shrimp is oriented with reference to gravity, and its dorsoventral axis approximately corresponds to the direction of this force. If the shrimp rotates around its chief axis either to right or left, say 90°, the direction of the pull of gravity on the statoliths is at once changed, and through the medium

[5] Verworn (47) first suggested the use of the word "statolith" instead of the word "otolith," which is generally used. The writer thinks it is desirable to accept Verworn's term.

of the latter other sensory hairs of the sac are stimulated. As a result, the shrimp turns back in a direction opposite to that in which it was rotated, until it is again in a normal relation to the direction of gravity. The employment of the magnet has no other effect than merely to change the direction of the orienting force. This is no longer that of gravity alone, but the *resultant* of the two component forces, gravity and the pull of the magnet. The animal now maintains its swimming position in reference to this new line of attraction, its dorso-ventral axis coincident with that line, and as a result the dorsal side is turned away from the magnet" (39, p. 240). Thus we can see that the pull of gravity on the statoliths in Palaemonetes plays an important rôle in the physiological function of equilibrium.

In connection with this, let us cite another interesting and important example from the same work. In lobsters, the larvae after ecdysis have no statoliths, and may be kept without them for one or two days, if they are placed at once after ecdysis into filtered sea-water. The effect of the lack of statoliths on the equilibrium of the animals can be thus observed. Within two hours after moulting, most of them swim about actively, and eat greedily when fed with bits of crab's liver. In swimming, however, they show quite marked abnormality. "There is both rolling from side to side, and 'pitching' forward and backward; often they swim with the ventral side uppermost. Much more easily overturned than normal larvae, they do not right themselves at once, but if turned upon the back, will continue to swim in that abnormal position. If blinded, the loss of equilibrium is still more marked. All these conditions are in strong contrast to the actions of the normal free-swimming larvae of these stages, which conduct themselves in the characteristic manner" (39, p. 238). These abnormalities, the result of the loss of equilibration, disappear at once when the larvae are allowed to obtain statoliths (39, p. 239). There is, therefore, no other explanation than that the statoliths, which are acted upon by the pull of gravity, maintain equilibrium in the line of the direction of gravity. This case is very important, because when we come to consider the geotropism of the higher vertebrates on which very extensive experiments have been made, we shall see that vertebrates deprived of their statoliths show the same abnormal phenomena manifested by lobster larvae without statoliths. This must be borne in mind.

III. Gravity, however, is not the only force which affects the behavior of animals. Many forces—light, contact stimulus, chemicals, temperature, and so forth, may act together. This leads to quite intricate results. Marine snails, for instance, which have statoliths, are naturally negatively geotropic.[6] But they are also negative to light. As affected by gravity, therefore, the animals are forced to crawl upward, but when exposed to light, they have to crawl downward. If the effective "strength" of gravity which depends on the position of the animals, is exactly equal to that of light, the animals might be stationary as a resultant of the two forces. If this is not the case, however, the stronger force might overcome the other. Gravity, of course, is constant—the pull of about 980 dynes—and always is exerted vertically. But the effective force exerted on the animals depends upon the position of the surface on which the animals may crawl. The exertion required to enable the animals to move on a horizontal surface is less than that required on a vertical surface, where the maximum force must be exerted. On the other hand, the intensity of light naturally changes, and can be artificially changed.

Suppose strong sunlight is falling vertically down, and the surface, on which the animals are crawling, is situated vertically. What direction must the animals take? The results of my experiments indicate that many of them—say 75%—crawl down. The light stimulus seems thus to be stronger than that of gravity. If you cover the vertical glass on which the snails are crawling down in direct sunlight with a dark box, you will be surprised to find the snails crawl upward in a few seconds; then, if you expose them to direct sunlight again, they will crawl down in a few seconds. They thus change their "minds" very rapidly!

Suppose again, we conduct an experiment in a room where there is no direct sunlight and place a vertical surface for the animals to move on. What must the animals do this time? Nearly all, if not all, crawl upward. Here is a problem for the psychologist, that is, a problem of "attention." Is that "attention" which causes an animal to go down or up, when it is stimulated by the relatively stronger of two stimuli focused by an idea or train of ideas? Other things being equal, is it true that the greater the intensity of an experience, the greater its clearness? Or, is "attention" something directed by physical and chemical changes which are

[6] A paper, "Studies on the Geotropism of the Marine Snail, Littorina Littorea," is ready for publication.

produced by the relative intensity of light or gravity in the protoplasm of the cells, especially in a photosensitive or geosensitive region?

This point will soon become clear if we consider the reversibility of geotropism and heliotropism in the larvae of the marine annelid, Arenicola cristata. The larvae are naturally negative to gravity and positive to light. If you add 25 cc. of isotonic $MgCl_2$ or $CaCl_2$ solution to 25 cc. of sea-water, and transfer Arenicola larvae in this mixture, about two minutes later they all become positive to gravity and swim downward, being oriented with their anterior ends in that direction, though their positive heliotropism seems not to be changed very much. Instead of $MgCl_2$ or $CaCl_2$, if you add 25 cc. of isotonic NaCl or weak acids to 25 or 50 cc. of sea-water, and transfer the larvae to this mixture, you will notice that the larvae become negative to light, though they, also, remain negative to gravity (24).

We may conclude that the change of the chemical composition, consequently of physical property, of the surrounding medium changes the geotropism and heliotropism of the larvae, although we do not yet know what change occurs in the organisms themselves.

Let us take another example to illustrate this point. We have already seen that Arenicola larvae become positive to gravity on addition of isotonic $MgCl_2$ or $CaCl_2$ solution to sea-water, though their light reaction is not affected very much. On the other hand, the larvae become negative to light on addition of isotonic NaCl solution to sea-water, though they remain negative to gravity. Now, it is well known among physiologists that $CaCl_2$ or $MgCl_2$ antagonizes the action of NaCl on organisms. In accord with this, if you add 5 cc. of isotonic $CaCl_2$ solution to the mixture of 25 cc. of isotonic NaCl and 25 cc. of sea-water, you will find that the reversibility of positive heliotropism of the larvae is very much retarded. What does this mean? This seems to mean that mutual antagonism of $CaCl_2$ and NaCl neutralizes the specific effect of each salt upon the larvae. This is physiologically of great significance. We seem therefore to be driven to the conclusion that both geotropism and heliotropism in animals are physico-chemical phenomena, and even such a problem as that of "attention," or the "initiative" of attention, as Royce expresses it, might be attacked by physico-chemical means instead of by entangled terms of consciousness (Cf. 10, 22, 41 and 48).

IV. It is well known that many insects show negative geotropism, but we cannot dwell on it here. So let us briefly

consider geotropism in still higher animals—the vertebrates, including mammals and man. Since Flourens experimentally showed in 1824 that extirpation of the vestibule and semicircular canals caused marked disorders of equilibration, immense energy has been spent by physiologists upon the problem of a sense of equilibrium in fishes, birds, rats, dogs, cats, etc. In normal animals the statoliths which are analogous to those of lower animals are present in the utriculus and sacculus. That the incidence of the pressure of the statoliths on the hairs will vary according to the position of the animal, so that any change in the position of the head will be at once attended by alteration in the nerve fibres which have been stimulated by the pressure of the statoliths (Cf. 46, pp. 449-450), and therefore in the nature of the impulses regulating the locomotion and the maintenance of the equilibrium of the animal (a theory agreed to by most, but not all, investigators) has been already considered in reference to the "iron statoliths" of Palamonetes, to attract which a strong electromagnet is employed.

On the other hand, the animals—fishes, birds, or dogs—which are deprived of the statoliths, or in which the semicircular canals have been destroyed, show inability to coördinate the muscles used in standing, locomotion, or flying. "The character and extent of these results vary with the number of canals injured, and indeed, show a more or less definite relationship to the several canals. When the horizontal canal is cut on one side in pigeons, the animal makes movements of the head in the plane of that canal, and if the similar canal on the other side is also sectioned, these movements are more pronounced." "When all three canals are cut on one or both sides, the animal shows a distressing inability to maintain a normal position. The head is twisted, it is not able to stand unless supported, and any attempt at walking or flying results in violent forced and incoördinated movements. The animal makes continued somersaults at each attempt to stand or walk, and the head is kept in spasmodic, forceful movements, which may produce injury or death." "It should be added that results of this character are obtained only when the membranous canals are injured. If the bony canal alone is cut, and even if the perilymph is removed by suction, no such effects are obtained" (21, pp. 399-400). These descriptions remind us of the observations on lobster larvae, already referred to, which were kept without statoliths.

In man, as in the shrimp, it is the statolith organ which determines the behavior in relation to the force of gravity. The statolith organ is therefore responsible in part at least,

not only for the maintenance of equilibrium, but also for the sensations which enable a man to orient himself and to know the position in which he happens to be at any given moment. There has been, of course, no experimentation on man deprived of the statoliths, or with the semicircular canals destroyed. But clinical data (1 and 42) point to the same conclusion, and cats and dogs have served for further proof (43).

V. As indicated briefly above, the facts regarding injury to and stimulation of the semicircular canals and the statolith organs, are very numerous, and, on the whole, fairly concordant. Their interpretation, however, has offered great difficulties, and many views have been proposed. Almost every investigator, in fact, has, to some extent, varied in his interpretation of the precise functional significance of these organs. We can, therefore, understand why there are many theories concerning them.

But a consideration of the structure of the statolith organs[7] shows at once that the incidence of the weight of the statoliths on the hairs of the maculae in the utricle and saccule will vary according to the position of the head, or of the animal's body. The nerve-endings stimulated by the weight of the statoliths will therefore vary according to the position of the head, or of the animal. The impulses of the stimulated nerve-endings will flow to the central nervous system. A reaction of the animal will obviously be the result (46, p. 680-681).[8]

When we have thus considered, though very briefly, geotropism in animals from the unicellular organism to man, we can fairly understand what an important rôle as stimulus the force of gravity plays in the physiology of animals in general. Consciousness, on the other hand, seems to play little part in the orientation of animals to gravity.

Selected Bibliography

(The literature in question is too extensive to make any complete bibliography. The writer has, therefore, selected the following from a great number of articles which he has read.)

1. Ballenger, William L. (1914.) Diseases of the Nose, Throat, and Ear. Fourth ed. Philadelphia: Lea & Febiger. Pp. 601-1032.

[7] The semicircular canals must very probably be a part of the organ of static equilibrium. The eyes also have an important rôle in equilibration, but the writer has purposely omitted consideration of it in this paper.

[8] It seems to us therefore that the theory of Mach is of great significance.

2. BEER, THEODOR. (1898.) Vergleichend physiologische Studien zur Statocystenfunction. I. Ueber den angeblichen Gehorsinn und das angebliche Gehororgan der Crustaceen. Archiv f. d. ges. Physiol., Bd. 73, S. 1-40.
3. —— ——. (1899.) Vergleichend physiologische Studien zur Statocystenfunction. II. Versuche an Crustaceen (Penaeus membranaceus). Archiv f. d. ges. Physiol., Bd. 74, S. 364-382.
4. BETHE, ALBRECHT. (1894.) Ueber die Erhaltung des Gleichgewichts. Biol. Centralb., Bd. 14, Pp. 95,114, 563-582.
5. BRAUN, ALFRED, and FRIESNER, ISIDORE. (1913.) The Labyrinth. New York: Rebman Co. Pp. 250.
6. BREUER, JOSEF. (1890.) Ueber die Function der Otolithen-Apparate. Archiv f. d. ges. Physiol. Bd. 48, S. 195-306.
7. —— ——. (1897.) Ueber Bogengange und Raumsinn. Archiv f. d. ges. Physiol. Bd. 68, S. 596-648.
8. BROWN, A. CRUM. (1874.) On the sense of rotation and the anatomy and physiology of the semicircular canals of the internal ear. Jour. of Anat. and Physiol., Vol. 8, Pp. 327.
9. —— ——. (1889.) Our Sensations of Motion. Nature, Vol. 40. Pp. 449.
10. BURNHAM, WILLIAM H. (1908.) Attention and Interest. Am. Jour. Psychol., Vol. 19. Pp. 14-18.
11. CLAR–, GAYLORD P. (1894.) Ueber Gleichgewichtsphänomene Crustaceen. Centralb. f. Physiol. Bd. 8, No. 20, S. 626-631.
12. —— ——. (1896.) On the Relation of the Otocysts to Equilibrium Phenomena in Galasimus Pugliater and Platyonuhus Ocellatus. Jour. of Physiol., Vol. 19. Pp. 327-343.
13. DARWIN, CHARLES. (1885.) The Power of Movement in Plants. New York: D. Appleton Co. Pp. X + 592.
14. FRÖLICH, ALFRED. (1904.) Studien uber die Statocysten. I. Mittheilung. Versuche an Cephalopoden und Einschlagiges aus der menschlichen Pathologie. Archiv f. d. ges. Physiol., Bd. 102, S. 415-472.
15. —— ——. (1904.) Studien über die Statozysten wirbelloser Tiere. II. Mitteilung. Versuche an Krebsen. Archiv f. d. ges. Physiol., Bd. 103, S. 149-168.
16. —— ——. (1905.) Ueber den Einfluss der Zerstörung des Labyrinthes beim Seepferdchen nebst einigen Bemerkungen über das Schwimmen dieser Tiere. Archiv f. d. ges. Physiol., Bd. 106, S. 84-90.
17. GOLTZ, FR. (1870.) Ueber die physiologische Bedeutung der Bogengäng des Ohrlabyrinths. Archiv f. d. ges. Physiol., Bd. 3, S. 172-192.
18. GREEN, J. REYNOLDS. (1909.) A History of Botany (1860-1900). Oxford: Clarendon Press. Pp. 543.
19. HALL, G. STANLEY. (1897.) A Study of Fears. Amer. Jour. Psychol., Vol. 8. Pp. 154-160.
20. —— ——. (1914.) A Synthetic Genetic Study of Fear (III Psychic Geotaxy). Am. Jour. Psychol., Vol. 25. Pp. 321-330.
21. HOWELL, WILLIAM H. (1913.) A Text-Book of Physiology. Fifth ed. Philadelphia: W. B. Saunders Co. Pp. 1020.
22. JENNINGS, H. S. (1906.) Behavior of the Lower Organisms. New York: Macmillan Co. Pp. XIV + 366.
23. KANDA, SAKYO. (1914.) On the Geotropism of Paaramecium and Spirostomum. Biol. Bull., Vol. 26. Pp. 1-24.

24. ——. (1914.) The Reversibility of the Geotropism of Arenicola Larvae by Salts. Am. Jour. Physiol., Vol. 35. Pp. 162-176.
25. LEE, FREDERIC S. (1894.) A Study of the Sense of Equilibrium in Fishes. I. Jour. of Physiol., Vol. 15. Pp. 311-348.
26. ——. (1894.) A Study of the Sense of Equilibrium in Fishes, Part II. Jour. of Physiol., Vol. 17. Pp. 192-210.
27. ——. (1898.) The Functions of the Ear and the Lateral Line in Fishes. Am. Jour. Physiol., Vol. 1. Pp. 128-144.
28. LOEB, JACQUES. (1897.) Zur Theorie der physiologischen Licht and Schwerkraftwirkungen. Archiv f. d. ges. Physiol. Bd. 66, S. 439-466.
29. ——. (1905.) Studies in General Physiology. Part I. Chicago: The University of Chicago Press. Pp. 176-190, 191-205.
30. ——. (1906.) The Dynamics of Living Matter. New York: Columbia University Press. Pp. XI + 233.
31. ——. (1911.) Die Tropismen. Handbuch der Vergleichenden Physiologie. Bd. IV, Erste Häfte, S. 451. Jena, Gustav Fischer.
32. LYON, E. P. (1899.) A Contribution to the Comparative Physiology of Compensatory Motions. Am. Jour. Physiol., Vol. 3, 1910. Pp. 86-114.
33. ——. (1905.) On the Theory of Geotropism in Paramaecium. Am. Jour. Physiol., Vol. 14. Pp. 421-432.
34. ——. (1905.) Some Results of Centrifugalizing the Eggs of Arbacia. Am. Jour. Physiol., Vol. 15 (Proc. Am. Physiol. Soc., 1905. Pp. xxi-xxii).
35. ——. (1907.) Results of Centrifugalizing Eggs. Arch. f. Entw.-mek., Vol. 23. Pp. 151-173.
36. M'KENDRICK, JOHN GRAY, and GRAY, ALBERT A. (1900.) The Ear (the semicircular canals). Text-book of Physiol., Vol. II, ed. by E. A. Schafer. Edinburgh and London: Young J. Pentland. Pp. 1194-1205.
37. MASSART, JEAN. Versuch einer Einteilung der nicht nervösen Reflexe. Biol. Centralb., Bd. XXII, S. 9-23, 41-52, u. 65-79.
38. PFEFFER, W. (1906.) The Physiology of Plants. Vol. III. Sec. fully rev. ed. Tr. by Alfred J. Ewart. Oxford: Clarendon Press. Pp. VIII + 451.
39. PRENTISS, C. W. (1901.) The Otocyst of Decapod Crustacea—Its Structure, Development, and Functions. Bull. of Mus. Comp. Zool., Vol. 36. Pp. 165-251.
40. PRINGSHEIM, ERNEST G. (1912.) Die Reizbewegungen der Pflanzen. Berlin: Julius Springer. Pp. VIII + 326.
41. ROYCE, JOSIAH. (1904.) Outlines of Psychology. New York: Macmillan Co. Pp. XXVII + 392.
42. RUTTIN, ERICH. (1914.) Diseases of the Labyrinth. Tr. by Horace Newhart. New York: Rebman Co. Pp. VIII + 232.
43. WILSON, J. GORDON, and PIKE, F. H. (1912.) The Effects of Stimulation and Extirpation of the Labyrinth of the Ear, and Their Relation to the Motor System. Part I—Experimental. (Pl. 13-16.) Phil. Tr. Roy. Soc. of London, S. B. Vol. 203. Pp. 127-160.
44. SACHS, JULIUS VON. (1890.) History of Botany. (1530-1860.) Tr. by Henry E. F. Garnsey, and revised by Isaac Bayley Balfour. Oxford: Clarendon Press.

45. SEWALL, HENRY. (1883.) Experiments upon the Ears of Fishes with Reference to the Function of Equilibrium. Jour. of Physiology, Vol. 4. Pp. 339-349.
46. STARLING, ERNEST H. (1912.) Principles of Human Physiology. Philadelphia: Lea & Febiger. Pp. XII + 1423.
47. VERWORN, MAX. (1891.) Gleichgewicht und Otolithenorgan. Archiv f. d. ges. Physiol., Bd. 50, S. 423-472.
48. WASHBURN, MARGARET FLOY. (1908.) The Animal Mind. New York: Macmillan Co. Pp. X + 333.